Title: As clear as day: nocturnal activity differs from diurnal activity in a temporally constrained capital breeder

Short title: Diurnal and nocturnal behaviour differs in seals

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Summary

Time-activity budgets are fundamental to behavioural studies, allowing examination of how individuals allocate their time, and potentially energy, and how these patterns vary spatially and temporally and in relation to habitat, individual identity, sex, social status and levels of anthropogenic disturbance. Direct observations of animal behaviour, especially in the wild, are often limited to daylight hours, therefore many activity budgets relate to diurnal activity only, or assumptions are made about nocturnal activity. Activity budgets have been a key component of many behavioural and energetics studies of breeding grey seals (*Halichoerus grypus,* Fabricius 1791), and yet very little is known about nocturnal activity of grey seals, and a general, implicit assumption of no significant change from day to night seems to pervade the literature. Here we use a combination of high resolution digital video and thermal imaging video camera to follow known individual grey seal mothers from day into night to examine activity patterns during lactation. We show distinct differences in nocturnal activity budgets relative to diurnal activity budgets. Mothers spent significantly more time resting with a reduction of time spent in the alert and comfort move behavioural categories during nocturnal periods. It is clear that diurnal time-activity patterns of breeding female grey seals cannot be extrapolated to represent activity across a 24 hour cycle. These considerations are particularly critical in studies that aim to use time-activity budgets as proxies for energy budgets.

Keywords: grey seal, *Halichoerus grypus*, lactation behaviour, activity budgets, time-activity budgets, nocturnal

Introduction

Time-activity budgets are the foundation of many behavioural studies (Altmann, 1974), providing valuable information about how individuals allocate their time, and potentially energy, and how these patterns may change over time, across populations or among individuals in relation to sex, age, status, social context, topography, thermal environment (e.g. Anderson & Harwood, 1985; Isbell & Young, 1993; Klinka & Reimchen, 2002; Twiss et al. 2002), and more recently the impacts of anthropogenic activity (e.g. Bayne et al., 2008; Christiansen et al. 2013; Bishop et al. , 2015). Activity budgets are typically generated from direct visual observation, however, such observations are often limited to daylight periods, therefore many activity budgets relate to diurnal activity only, or assumptions are made about nocturnal activity (e.g. diurnal species may be assumed to rest at night). 24 hour activity budgets are more feasible in captive situations (e.g. Horback et al., 2014; Pépin et al., 2006), but may be of limited use for extrapolation to their wild counterparts (Dawkins, 1988; Birkett & Newton-Fisher, 2011), especially as behavioural ecologists typically seek to understand how behaviour is shaped by the selective forces operating on organisms in their natural environment (Cockrem, 2013).

Marine mammals are difficult to observe directly in the wild as many spend all their lives in water. Pinnipeds, however, use both marine and terrestrial habitats making them suitable for prolonged observation during terrestrial phases, especially the annual breeding season. Grey seals (*Halichoerus grypus,* Fabricius 1791) are capital breeders (fasting during breeding and relying upon reserves accumulated prior to breeding) with a discrete annual breeding season, during which females come ashore to give birth to a single pup, nurse and wean the pup, and mate within ca. 20 days, before returning to sea. How individual grey seals apportion their limited resources during this brief, intensive

period of pup rearing and mating has been intensively studied (e.g.: Anderson et al., 1975; Boness, 1984; Anderson & Fedak, 1985; Anderson & Harwood, 1985; Pomeroy et al.,1999; Twiss et al., 2000; Bishop et al., 2015), and activity budgets have been a key component of many of these behavioural and energetics studies. However, these studies only assessed diurnal activity, and either made no assumptions about nocturnal behaviour, or implicitly assumed that nocturnal behaviour did not differ from diurnal behaviour. Only two studies have compared diurnal and nocturnal behaviour in grey seals (Anderson, 1978; Culloch et al., 2016). Anderson (1978) focused on a single male for two breeding seasons and, although a decrease in vigilance at night was observed, concluded that diurnal and nocturnal behaviour were not significantly different. Culloch et al. (2016) observed five post-partum females and found that vigilance decreased and resting increased during night-time relative to day-time. However, because the same individuals were not always followed from day to night, the analysis was conducted at the group, rather than individual, level.

Our study aimed to clarify the extent of differences between diurnal and nocturnal behaviour in adult breeding female grey seals by following known individuals through day time and on into night-time periods using focal sampling protocols. It was important that the study be at the individual-level because substantial individual variation in behaviour is known for grey seals during the breeding season (Twiss et al., 2012). Here, we use General Linear Mixed Models (GLMMs) to test whether specific behaviours show a significant change in time allocation or remain the same across diurnal and nocturnal periods.

Material and Methods

Ethical statement

This study was purely observational in nature and all work was approved by Durham University Animal Welfare Ethical Review Board and complied with ASAB/ABS ethical guidance and conformed to UK legislation under the Animals (Scientific Procedures) Act 1986 Amendment Regulations (SI 2012/3039).

Study Colony and Site

The Isle of May is a small island situated 5 kilometres off the East coast of Scotland at the mouth of the Firth of Forth (56.19ºN, 2.57ºW). The grey seal colony on the island is comprised of over 2,000 adult females with approximately 2,000 pups born each year on the island (SMRU, 2017). The breeding season on the island spans late October to mid-December with most births occurring during November. The study site used for data collection is a small area to the South East of the island known as Crosspark. The site is approximately 2,200 m^2 in size and is made up of undulating grassy substrate with rocks randomly distributed around the site. All observations were recorded from a wooden observation hide located in the North-West junction of the surrounding stone walls.

Selection of behaviour categories

We predicted that lactating female grey seals would spend relatively more time resting during nocturnal compared to diurnal periods, as suggested by Culloch *et al*. (2016). We also predicted that females would reduce the amount of time spent alert (vigilant) during nocturnal periods, as visual scanning of their environment will be less

effective in the dark. Likewise, we anticipated a reduction in aggression during nocturnal periods as individuals are less active and are therefore less likely to come into contact with conspecifics. We also selected two behavioural categories that we predicted would not exhibit differences in the proportion of time devoted to these activities across diurnal and nocturnal periods: First, the combined category of Presenting and Nursing, representing mothers attempting to provision their pup, the primary purpose of their sojourn ashore during the breeding season. As female grey seals have a discrete, limited time frame over which to provision their pups, and weaning mass equates to offspring survival (Hall et al., 2002), it seems probable that mothers would not reduce provisioning rates simply due to darkness (Kovacs, 1987). Finally, we selected Comfort Moves, sporadic adjustments of the resting position of females, which we had no *a priori* reason to assume would change in frequency or duration of occurrence during diurnal or nocturnal periods.

Behavioural Data Collection

Behavioural observations were carried out on 30 days between 26th October and 25th November 2015. Before observation began, individuals were identified using unique pelage markings on each seal (Twiss et al., 2000; Redman et al., 2001). One observer (ZLF) performed all individual identifications and observations. Photographs of all individuals in the study site were taken using a Canon EOS 450 camera with a 120-400mm lens and a daily catalogue of ID photographs was maintained. As grey seal pups age they can be classified into discrete developmental stages (pup stages I-V; Kovacs & Lavigne, 1986), which can be used to approximate age. During each observation day all pup developmental stages were recorded. Pups at stages I and II were classed as young (Y) and those at stages III, IV and V were classed as old (O).

141 Diurnal and nocturnal periods were defined based on times of sunrise and sunset
142 derived from https://www.timeanddate.com/sun/uk/edinburgh (accessed: 15/08/17).
143 Diurnal focal video observations were recorded using a Canon LEGRIA HF R36 HD
144 camcorder with a 32x optical zoom. Diurnal observations began up to 3.5 hours before
145 sunset. Focal seals were observed from diurnal into nocturnal periods to ensure
146 individuals' ID was known. All nocturnal observations were performed from sunset till up
147 to 5.25 hours after. Nocturnal observations were recorded using a FLIR, PHOTON 640
148 PAL camera (resolution: 640x480 pixels; zoom: x4). The distance of the focal individual
149 from the camera varied from 35m to 90m for both diurnal and nocturnal observations.

150

151 *Behavioural Data Extraction and Analysis*

152 A total of 73h of diurnal and 68h of nocturnal video footage were recorded that
153 included 20 mothers, of these only 11 individuals had both diurnal and nocturnal focal
154 videos; only these data were used for statistical analysis. Due to the positioning of
155 individuals around the site, and our prioritisation of maximising the number of identified
156 individuals observed, together with the lower number of nocturnal videos, few individuals
157 had three or more diurnal or nocturnal focal videos (Table 1).

158 Diurnal and nocturnal video footage was decoded using a focal sampling protocol
159 (Altmann, 1974) and a bespoke Visual Basic for Applications Macro in Microsoft Excel,
160 to record behaviours based on the ethogram presented in S1 (supplementary information).
161 All videos were decoded by the same observer (ZLF). Videos with more than one focal
162 individual in them were watched once for each individual present in the video. The order
163 of decoding was conducted randomly with respect to individual, date of recording and
164 whether the footage was from diurnal or nocturnal periods. Periods when observed

individuals were out of sight of the video cameras were removed prior to analysis. If the observed individual left the video frame during night observations, their observation period was stopped once the entire body had left the frame. For each individual, the proportions of time spent in each behaviour were established for each of their focal videos. Data were then aggregated into coarser behaviour categories where appropriate:

The categories Resting and Comfort Move were as described in S1 and were derived directly from the decoded data. Presenting included Presenting-Alert (where the mother was simultaneously Presenting and Alert; see S1), and Alert also included Presenting-Alert (as the mother is in a state of vigilance despite Presenting). It is important to note that it is difficult to directly observe when a pup is actively acquiring milk from its mother, even where the pup is in oral contact with the mother's nipples (Nursing), especially at night. Therefore, our Presenting category represents a combination of Presenting and Nursing. We cannot say anything about potential differences in energy transfer to the pup during day or night, as even direct observations of Nursing do not predict milk transfer well (Mellish et al. 1999; Pomeroy et al. 1999). Aggressive behaviours (see S1) were combined into a single group, Aggression.

To test our predicted effects of diurnal/nocturnal periods on time-activity budgets we constructed General Linear Mixed Models (GLMMs) in R 3.5.0 (R Core Team, 2018) using the glmmTMB package (Brooks et al. 2017). Response variables were the proportion of time that individuals spent within each of the behaviour categories of interest per video focal. We constructed separate models for each of the behavioural categories Resting, Alert, Presenting, Comfort Move and Aggression. Some individuals showed zero values for the behavioural categories Aggression and Presenting, so the data were shifted by adding the minimum non-zero value for each category respectively, allowing for logit-transformation (Warton & Hui, 2011). All response variables were

checked for normality using Q-Q plots. Potential explanatory variables in our models were: Pup age class (Y, O), which was included because previous studies have suggested that female behaviour changes as pups age (Kovacs, 1987). Date (expressed as the number of days from the 1st October 2015) was included as an independent variable to account for gross changes in behaviour as the breeding season progresses due to changes in the numbers of conspecifics. We included Date as a polynomial term as the numbers and density of seals on the breeding colony increase to a peak mid-season (mid-November), and then dwindles again, and we anticipated that individual activity patterns would respond to these gross changes in colony dynamics. Individual ID was included as a random effect to account for serial correlation, and to account for variation that is caused by differences between individuals within the population (Pinheiro & Bates, 2000; Bolker et al., 2009). To account for the different amount of sampling effort per individual per focal, each data point was weighted according to the duration of the focal sample. Finally, we included the effect of diurnal/nocturnal to test if this influenced the proportion of the behaviour observed. We also included the potential interaction between pup age class and diurnal/nocturnal because pup vulnerability to conspecific aggression, or from marauding gull will potentially change with age (Kovacs 1987; Twiss et al. 2003) and with light levels due to changes in seal activity. Consequently, maternal behaviour may reflect these changes in risk to the pup.

For each response variable, the modelling procedure began by fitting full (global) models, using the binomial family and logit link appropriate for proportional data. To account for potential overdispersion in the models, we also constructed alternate full models for each response variable using the beta-binomial distribution, which is a compound distribution of the binomial distribution with the Beta distribution that allows for heterogeneity in per-trial probability (Bolker, 2008, Brooks et al. 2017). We tested for

overdispersion by comparing full models for both the binomial and beta-binomial distributions, for each behavioural category, using Akaike Information Criterion, corrected for small sample size (AICc; Anderson, 2008) with the AICctab function in the 'bblme' package in R (Bolker et al. 2017). For all response variables the beta-binomial version outperformed the binomial version, with reductions in AICc of at least 2,677. Therefore, the beta-binomial distribution was deemed more suitable for these data.

For model inference, we examined alternate beta-binomial models with reduced combinations of explanatory variables using the R function 'dredge' from the Package '*MuMIn*' (Bartoń 2014). This approach avoids stepwise regression, which is often criticised (Whittingham et al., 2006). The model with the lowest corrected Akaike's information criterion (AICc) was chosen as the 'best' model, but we also retained and examined all models within a confidence set, which was defined following the criteria set out by Richards (2008); all models within a ΔAICc $\leq$6 of the 'best' model were retained within a preliminary confidence set. We then subsetted this initial confidence set, retaining only models that had a ΔAICc value lower than all the more complex models within which they were nested. This approach avoids retaining overly complex models but also acknowledges that the model with the lowest AICc score is not necessarily the most parsimonious model (Richards, 2008, Richards et al., 2011). For each of the models we also provide the output from the null model for comparison.

Results

Average time-activity budget data for all 11 individuals used for statistical analysis showed similar overall patterns for the proportions of time allocated to each behavioural category during both diurnal and nocturnal observations (Table 2). Both diurnal and

239 nocturnal activity were dominated by Resting (Day: 0.770± 0.022, Night: 0.843±0.023)
240 with Comfort Move, Presenting, Alert, and then Aggression accounting for decreasing
241 proportions of the activity budgets for both diurnal and nocturnal periods (Table 2).

242 GLMMs showed a significant effect of diurnal/nocturnal on the proportion of time
243 mothers spent Resting ($P = 0.03$), Alert ($P < 0.001$) and engaged in Comfort Moves ($P =$
244 0.005) (Table 3 and 4). The best models for Resting and Alert retained only
245 diurnal/nocturnal as an explanatory variable, while the best model for Comfort Moves
246 included diurnal/nocturnal and date (Table 3). Examining the effect sizes and directions
247 for the best models (Table 3), the proportions of time spent Resting was greater during
248 nocturnal relative to diurnal periods (Figure 1a). Conversely, the proportions of time spent
249 Alert, or engaged in Comfort Moves, declined during nocturnal relative to diurnal periods
250 (Figure 1b and 1c respectively). The proportion of time spent engaged in Comfort Moves
251 also increased as the breeding season progressed from early to mid-season (Table 3,
252 Figure 2). [Fig. 1 here]. [Fig. 2 here].

253 There was no effect of diurnal/nocturnal on the proportion of time mothers spent
254 Presenting or involved in Aggression, with the null model being the only model retained
255 in the confidence sets for these two behavioural categories (Table 4). Pup age had no
256 clearly discernible effect on the proportion of time mothers spent in any of the behavioural
257 categories. Even in the alternative model for Comfort Moves (Alternative 3, Table 4) the
258 effect of Pup age was small (estimate = -0.34± 0.22, $P = 0.12$), suggesting a marginal
259 decrease in Comfort Moves among mothers with older pups.

260

261 **Discussion**

This study shows clearly that time-activity budgets of lactating female grey seals differ between diurnal and nocturnal periods. As predicted, activity was found to decrease during nocturnal periods with an increase in Resting and a reduction in vigilance behaviour (Alert). This supports and extends the results found by Culloch et al. (2016). However, we also found a reduction in time spent in Comfort Moves during nocturnal periods, contrary to our prediction that Comfort Moves would remain at a similar level during both diurnal and nocturnal periods. By following known individuals from diurnal observation continuously through to nocturnal periods we have shown that individual seals do alter their behaviour across these periods, and that any diurnal-nocturnal effect on measured behaviour is not due to different samples of seals being observed in each period. This is an important distinction, as it is known that wild grey seals exhibit high levels of inter-individual variation in behaviour (Twiss et al., 2012).

The reduction in activity (non-Resting time) and vigilance in nocturnal periods could be a direct product of the visual acuity of grey seals. Pinniped vision is better in water than in air, however, during daylight hours they have been shown to have almost as good vision in air as in water (Riedman, 1990; Schusterman, 1975). When light levels are low however, visual acuity decreases in both water and in air (Schusterman, 1975). The detection of light during nocturnal periods is enhanced in grey seals due to their relatively thick *tapetum lucidum* compared to most other pinnipeds and some terrestrial mammals (Griebel & Peichl, 2003; Ollivier et al., 2004), however their ability to distinguish colour and fine detail is diminished (Riedman, 1990). This, along with the increased near-sightedness due to pupil dilation at low light levels, may restrict their ability to detect visual stimuli during nocturnal periods. Reduced visual acuity at night could also limit the ability of mothers to relocate their pup if they are separated. However, phocid seals have high olfactory sensitivity in air and good hearing, both important for mothers finding their

pups (Riedman, 1990). Nonetheless, mothers may reduce their activity during hours of darkness to maintain proximity to their pup and minimise the chances of losing their pup.

One might expect that with a reduced ability to perceive visual stimuli that warn of approaching threats, seals would startle when conspecifics encroach upon them during nocturnal periods. A general increase in Resting of all seals during nocturnal periods may reduce the likelihood of conspecific interactions, although we found no evidence of a nocturnal reduction in time spent in Aggression relative to diurnal periods. However, as noted above, reliance on other sensory modes may compensate for reduced visual acuity in darkness.

Thermoregulation may also affect the pattern of activity during diurnal and nocturnal periods. Female grey seals will travel to pools of water during to thermoregulate (Redman et al., 2001; Twiss et al., 2002) and drink (Stewart et al., 2014). Data from a regional meteorological station (Cellardyke, Anstruther, Fife; sourced from https://www.wunderground.com/) shows that during our study, diurnal temperatures were on average higher than nocturnal temperatures (mean diurnal temperature = 8.8±0.33^{o}C, mean nocturnal temperature = 7.3±0.34^{o}C). During diurnal periods, higher temperatures would be expected to increase the requirement to go to pools, leading to increased diurnal activity compared to nocturnal periods. As activity increases, heat production also increases creating a greater need for heat loss to maintain a stable body temperature. The requirement for thermoregulation during the hottest part of the day has been shown to affect behaviour in other pinniped species (Shipley & Strecker, 1986), therefore, cooler temperatures during nocturnal periods may permit an increase in Resting.

We predicted that Presenting and Comfort Moves would represent a similar proportion of the time-activity budget for both diurnal and nocturnal periods. This was

311 indeed the case for Presenting, however, time spent in Comfort Moves decreased in
312 representation during nocturnal observations. The reduction in time spent in Comfort
313 Moves is perhaps also explicable in terms of thermoregulation, with higher diurnal
314 temperatures causing more discomfort for seals. The general increase in Comfort Moves
315 with date may be attributable to the depletion of sub-cutaneous blubber reserves as
316 females progress through lactation, leading to more discomfort for seals lying on typically
317 rocky terrain.

318 This study used females from one site which covered only one habitat type.
319 Habitat type has been shown to affect activity in grey seals (Anderson & Harwood, 1985;
320 Kovacs, 1987; Redman et al., 2001; Twiss et al., 2000) and could therefore influence time
321 allocation among different behaviours in different habitats. However, it seems likely that,
322 even with gross differences in time-activity budgets driven by topography, diurnal and
323 nocturnal differences may remain, particularly in vigilance and Resting. This possibility is
324 supported by the findings of Culloch et al. (2016) whose absolute proportions of activity
325 varied from those calculated in this study but revealed the same pattern of increased
326 Resting during nocturnal observations compared to diurnal observations. It should be
327 noted that the observations made in our study extended up to 5 hours outside of diurnal
328 hours (to approximately 22:00 GMT), and so activity patterns for the remainder of the
329 nocturnal period remains unknown. However, this study has clearly shown that diurnal
330 activity patterns of breeding female grey seals cannot be extrapolated into nocturnal
331 periods, which, in an autumnal breeding season, account for two thirds (or more) of the 24
332 hour cycle. Mean time spent in Resting increased by 7% from diurnal to nocturnal periods,
333 which is not an insubstantial portion of a time-activity budget, especially in a situation
334 such as the grey seal breeding season, where females have a fixed energy reserve to draw
335 upon during lactation and expending too much in one breeding attempt can have negative

fitness consequences for subsequent breeding efforts (Pomeroy et al. 1999). Assuming equality of diurnal and nocturnal activity could lead to important miscalculations of time-activity budgets, which may be particularly important to consider in studies that aim to use time-activity budgets as proxies for energy budgets (Anderson & Fedak, 1985; Anderson & Harwood, 1985; Christiansen et al. 2013).

Acknowledgements

The authors would like to thank Simon Moss and Matt Bivens of the Sea Mammal Research Unit for extensive help during fieldwork. We also thank Courtney Shuert and Dr Amy Bishop for their thoughts and advice on fieldwork and during analysis. Funding for this work was provided by Durham University.

Declarations

Availability of data and materials

The data used and analysed in this study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

SDT conceived of the study and led the field work. ZLF collected the data and performed the analyses with support from SDT and RMC. SDT and ZLF wrote the paper with input from all co-authors. All co-authors read and approved the final manuscript.

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Tables

Table 1: The number of diurnal and nocturnal focal videos per individual for the 11 individuals used in statistical analysis.

	Number of Videos	
Individual ID	**Diurnal**	**Nocturnal**
Ind1	4	3
Ind27	2	1
Ind29	2	2
Ind30	2	2
Ind32	4	2
Ind33	4	3
Ind35	2	2
Ind42	1	1
Ind46	1	1
Tag4	1	1
Tag5	1	1

506 **Table 2:** Mean proportion of time spent in the behavioural categories examined (with
507 standard error, SEM). Number of focal sessions = 24 (diurnal) and 17 (nocturnal).
508 Note: proportions do not summate to 1 as (i) not all behavioural categories were
509 examined (see S1) and (ii) the simultaneous behaviour of Presenting-Alert is
510 included in both the Alert and the Presenting category.

	Mean proportion of time spent in category (±SEM)	
Behavioural category	**Diurnal**	**Nocturnal**
Resting	0.77(0.022)	0.843(0.023)
Alert	0.033(0.005)	0.013(0.003)
Aggression	0.008(0.003)	0.004(0.002)
Comfort Move	0.135(0.015)	0.078(0.011)
Presenting	0.043(0.008)	0.050(0.013)

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513 **Table 3:** Summaries of the best model for each of the behavioural categories investigated.
514 Diurnal is the reference state in the Diurnal/Nocturnal factor. Date is polynomial. Only
515 covariates that were retained within the best model are presented.

Response Variable	Independent Variables	Estimate	Standard Error	Z Value	P Value
Resting	Intercept	1.22	0.12	10.02	<0.001
	Diurnal/Nocturnal	0.43	0.20	2.17	0.03
Alert	Intercept	-3.39	0.13	-25.80	<0.001
	Diurnal/Nocturnal	-0.88	0.23	-3.76	<0.001
Comfort Moves	Intercept	-1.94	0.10	-18.68	<0.001
	Diurnal/Nocturnal	-0.49	0.17	-2.84	0.005
	Date	1.59	0.59	2.70	0.007
	Date ^{2}	-1.48	0.61	-2.40	0.016
	Date^3	0.62	0.55	1.13	0.29

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Table 4: Summary of all models (and null models) retained in the confidence sets for all behavioural categories investigated; the null model does not contain any covariates (-), models are ranked by the ΔAICc value, where 0 = the best model. The covariates retained within each model retained within the confidence set are listed.

Behaviour	Models	Intercept	Covariates	logLik	ΔAICc
Resting	Best Model	1.22	Diurnal/Nocturnal	-342.93	0
	Null Model	1.39	-	-345.23	2.13
Alert	Best Model	-3.39	Diurnal/Nocturnal	-263.74	0
	Null	-3.68	-	-270.56	11.19
Presenting	Null	-3.04	-	-292.08	0
Comfort Moves	Best Model	-2.04	Diurnal/Nocturnal + poly(Date)	-314.63	0
	Alternative 1	-1.92	Diurnal/Nocturnal	-320.08	2.61
	Alternative 2	-2.12	Date	-318.5	4.81
	Alternative 3	-2.05	Pup Class + poly(Date)	-317.24	5.21
	Null	-2.11	-	-323.61	7.22
Aggression	Null	-5.01	-	-207.19	0

logLik = Log likelihood, poly(Date) = polynomial term for Date.

Figures:

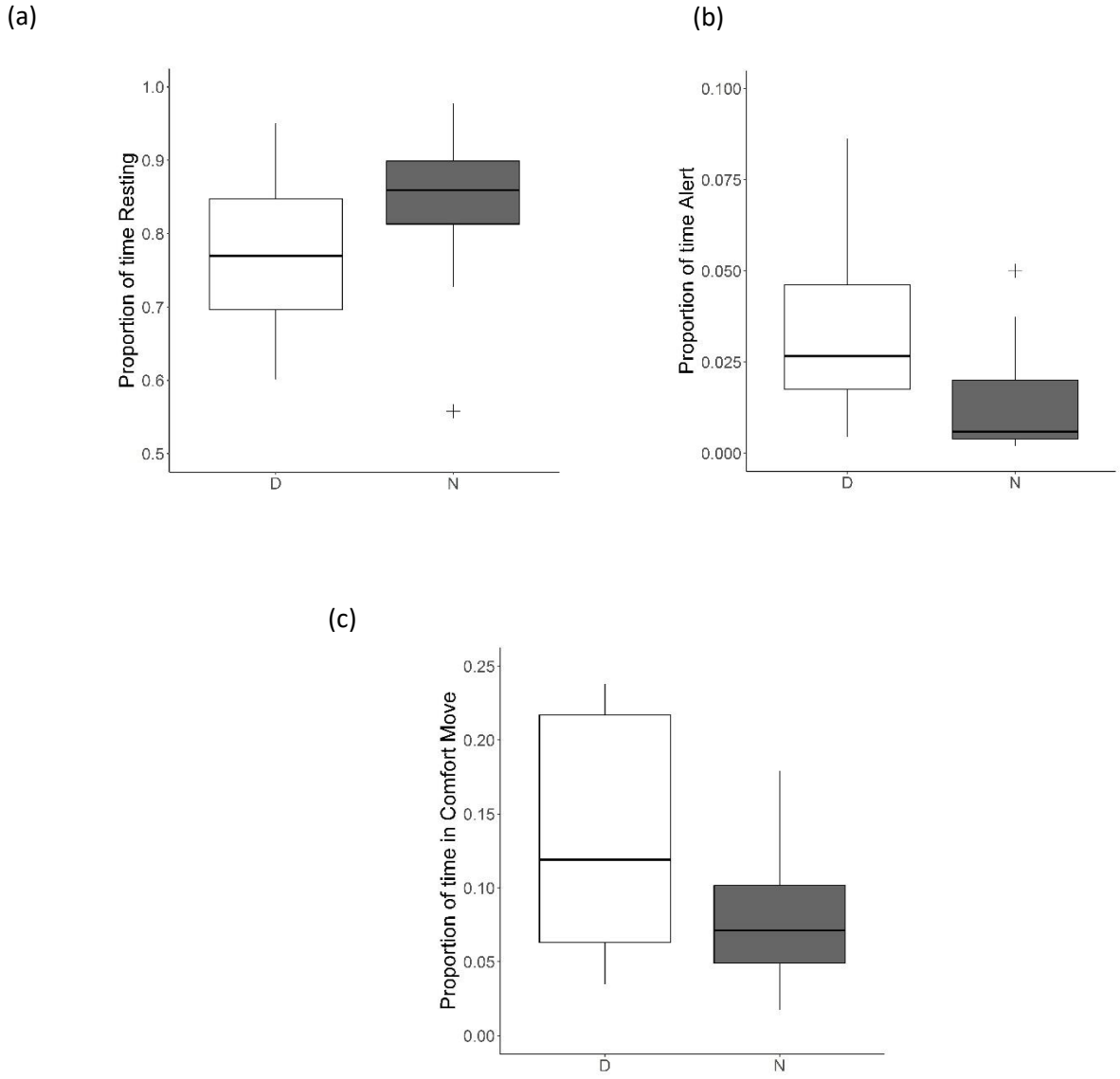

Figure 1. Boxplots depicting differences in proportion of time spent in the behavioural categories during diurnal (D) and nocturnal (N) observations. Behavioural categories are; (a) Resting, (b) Alert, (c) Comfort Move. Data values are the observed data rather than fitted values. Boxplots provide the median (black line) and interquartile range (box length), while the whiskers represent the most extreme data point which is no more than 1.5 times the length of the box away from the box. Outliers are denoted by +.

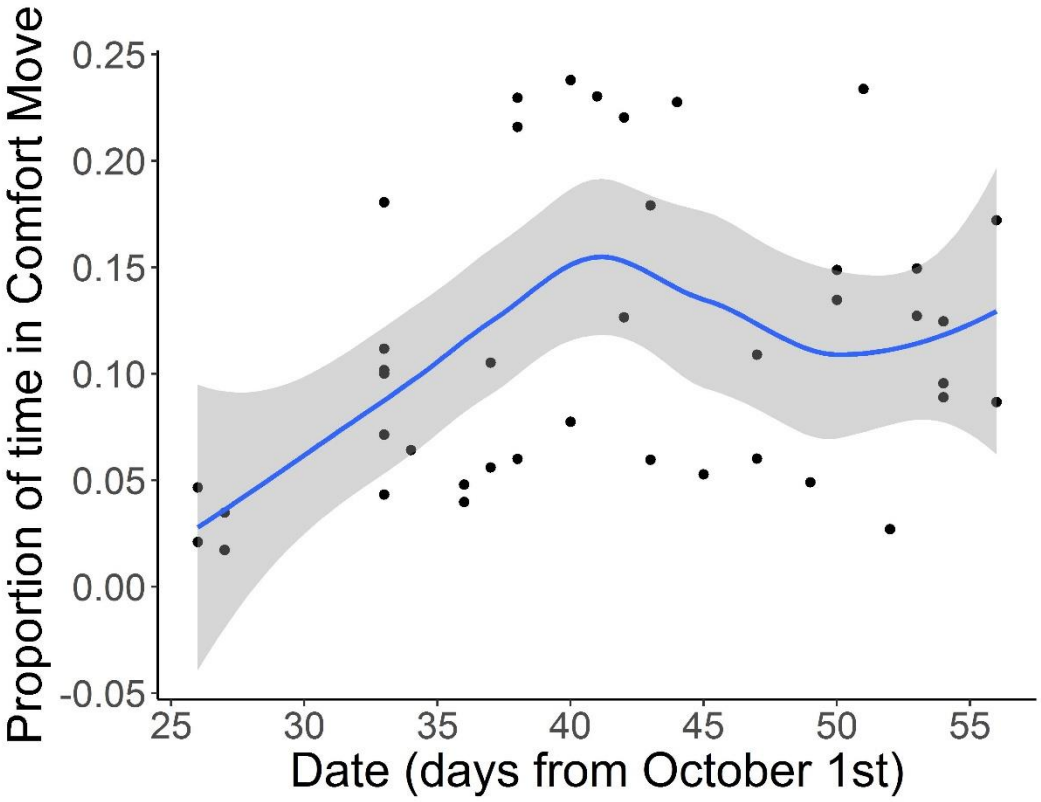

Figure 2. Variation in proportion of time spent in the Comfort Move behavioural category across dates. Line represents a Loess smooth, and the shaded area represents 95% confidence intervals.